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In this paper we realistically model a two-eye visual environment and study its effect on single cell synaptic modification. In particular, we study the effect of image misalignment on receptive field formation after eye opening. We show that binocular misalignment effects PCA and BCM learning in different ways. For the BCM learning rule this misalignment is sufficient to produce varying degrees of ocular dominance, whereas for PCA learning binocular neurons emerge in every case. Network results seem dominated by single cell results. Such differences should help us distinguish between these learning rules.

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Effect of Eye Misalignment on Ocular Dominance according to BCM and PCA Synaptic Modification

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Abstract

In this paper we realistically model a two-eye visual environment and study its effect on single cell synaptic modification. In particular, we study the effect of image misalignment on receptive field formation after eye opening. We show that binocular misalignment effects PCA and BCM learning in different ways. For the BCM learning rule this misalignment is sufficient to produce varying degrees of ocular dominance, whereas for PCA learning binocular neurons emerge in every case. Network results seem dominated by single cell results. Such differences should help us distinguish between these learning rules.

1   Introduction

It is now generally accepted that receptive fields in the visual cortex of cats are dramatically influenced by the visual environment (For a comprehensive review see, Frégnac and Imbert, 1984) . In normally reared animals, the population of sharply tuned neurons increases monotonically, whereas for dark reared animals it initially increases, but then almost disappears (See, for example, Imbert and Buisseret, 1975) . Ocular dominance is dramatically influenced by such manipulations as monocular deprivation (Wiesel and Hubel, 1963) or reverse suture (Blakemore and Van-Sluyters, 1974; Mioche and Singer, 1989). It has even been shown that preferred orientations can be directly altered by pairing the preferred orientation with a negative current, and the non-preferred orientation with a positive current (Frégnac et al., 1992).

Different models, that attempt to explain how cortical receptive fields evolve, have been proposed over the years (von der Malsburg, 1973; Nass and Cooper, 1975; Perez et al., 1975; Bienenstock et al., 1982; Linsker, 1986; Miller, 1994, e.g.). Such models are composed of several components: the exact nature of the learning rule, the representation of the visual environment, and the architecture of the network.

Most of these models assume a simplified representation of the visual environment (von der Malsburg, 1973, for example), or a second order correlation function of the visual

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environment (Miller, 1994). Realistic representations of the visual environment have only very recently been considered (Hancock et al., 1992; Law and Cooper, 1994; Liu and Shouval, 1994; Shouval and Liu, 1995). Furthermore, only in recent years have the statistics of natural images been studied, and compared with neurophysiological findings (Field, 1987; Field, 1989; Baddeley and Hancock, 1991; Atick and Redlich, 1992; Ruderman and Bialek, 1993; Liu and Shouval, 1994; Shouval and Liu, 1995).

In this paper, we realistically model a two-eye visual environment. We study how orientation selectivity and ocular dominance form simulatneously in both single cells and networks. In particular, we study the effect of image misalignment between the two eyes on receptive field formation [1].

We compare the effect of such image misalignment on two different learning rules PCA (Oja, 1982) and BCM (Bienenstock et al., 1982; Intrator and Cooper, 1992). We have chosen to examine these two because they are well defined and and have stable fixed points. Many other proposed learning rules (Sejnowski, 1977; Linsker, 1986; Miller et al., 1989, for example), are closely related to the PCA rule. Their outcome depends only on first and second order statistics. The BCM rule in contrast depends also on third order statistics.

We show that binocular misalignment has very different effects on these two learning rules. For the BCM learning rule misalignment is sufficient to produce varying degrees of ocular dominance, whereas for the PCA learning rule binocular neurons will emerge independent of the misalignment.

2 A Binocular Visual Environment Composed of Natural Images

We have used a set of 24 natural scenes. These pictures were taken at Lincoln Woods State Park and scanned into a 256×256 pixel image. We have avoided man-made objects, because they have many sharp edges, and straight lines, which make it easier to achieve oriented receptive fields.

We have chosen to model the effect of the retinal preprocessing by convolving the images with a difference of Gaussians (DOG) filter, with a center radius of one pixel ($\sigma_1 = 1.0$) and a surround radius of three ($\sigma_2 = 3$)[2]. The effect of this preprocessing is shown in figure 1.

As illustrated in Figure 2, the input vectors from both eyes are chosen as small, partially overlapping, circular regions of the preprocessed natural images; these converge on the same cortical cell.

The input from the right and left eye respectively are denoted by $\mathbf{d}^l$ and $\mathbf{d}^r$, and the output of the cortical neuron then becomes $c = \sigma(\mathbf{d}^l \cdot \mathbf{m}^l + \mathbf{d}^r \cdot \mathbf{m}^r)$, where σ is the non linear activation function of each neuron. We have used a nonsymmetric activation function to account for the fact that neuronal activity as measured from spontaneous activity has a longer way to go up than to go down to zero activity.

In order to examine the effect of varying the overlap between the receptive fields we define an overlap parameter $O = s/2a$, where a is the receptive field radius in pixels, and s is

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[1]Postnatal plasticity may be needed in animals with binocular vision, as was already suggested by Blakemore and van Sluyters (1975), in order to overcome an imprecise developmental alignment.

[2]This ratio between the center and surround in biologically plausible, and enables the PCA rule to produce oriented receptive fields.
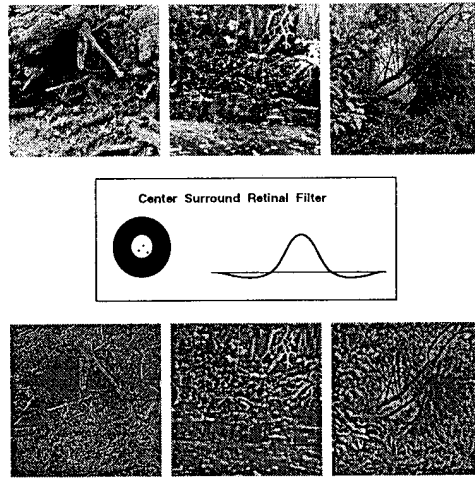
2

Figure 1: Three of the natural images used (top) processed by a Difference of Gaussians filter and presented at the bottom.
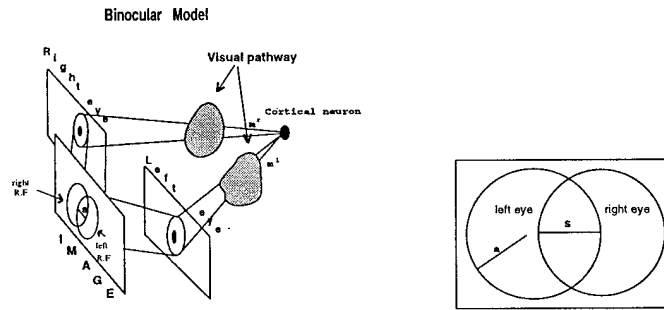

Figure 2: Schematic diagram of the two eye model, including the visual input preprocessing.

the linear overlap in pixels, as shown in Figure 2. When the left and right receptive fields are completely overlapping $O = 1$, when they are completely separate $O \leq 0$.

In order to asses the degree of cell binocularity, we introduced an ocular dominance measure B based on left and right eye response: $B = (L - R)/(L + R)$. B is calculated by first finding the orientation at which the cell has the greatest binocular response to a sinusoidal grading, and then measuring L and R, the left and right eye responses at that orientation.

This measure has been motivated by that used by Albus (1975) in defining the bin boundaries, for a seven bin ocular dominance histogram. Since there is always some activity from both eyes, we have extended bin 1 and 7 slightly. Our bin boundaries are given by: $-.085, -0.5, -0.15, 0, 15, 0.5, 0.85$.

3   Cortical plasticity learning rules

We have employed these realistic visual inputs to test two of the leading visual cortical plasticity rules that have been used to model various normal rearing and visual deprivation experiments: Principal components analysis (PCA) and the Bienenstock Cooper and Munro (BCM) model.

The two algorithms differ by their information extraction properties as discussed in Intrator and Cooper (1994); PCA extracts second order statistics from the visual environment, while BCM extracts information contained in third order statistics as well.

3.1 Principal Components Analysis

Principal components analysis (PCA) is one of the most widely used feature extraction method for pattern recognition tasks. PCA features are those orthogonal directions which maximize the variance of the projected distribution of the data. They also minimize the mean squared error between the data and a linearly reconstructed version of it based on these projections. Principal components are optimal when the goal is to accurately reconstruct the inputs. They are not necessarily optimal when the goal is classification and the data is not normally distributed (see for example, p. 212, Duda and Hart, 1973).

A simple interpretation of the Hebbian learning rule, is that with appropriate stabilizing constraints it leads to the extraction or approximation of principal components. This has often been modeled (See for example; von der Malsburg,1973; Sejnowsky, 1977; Oja, 1982; Linsker, 1986; Miller et. al., 1989) . The learning rule that we use has been proposed by Oja (1982), and has the form: $\Delta m_i = \eta[d_i c - c^2 m_i]$ where d_i is the presynaptic activity at synapse i, c is the postsynaptic activity, and m_i is the strength of the synaptic efficacy of junction i. η, is a small learning rate. This learning rule has been shown to converge to the principal component of the data.

3.2 BCM learning rule

The BCM theory (Bienenstock et al., 1982) has been introduced to account for the striking dependence of the sharpness of orientation selectivity on the visual environment. We shall be using a variation due to Intrator and Cooper (1992) for a nonlinear neuron with a nonsymmetric sigmoidal transfer function. Using the above notation, the synaptic modification is governed by $\dot{m}_j = \eta\phi(c, \Theta_M)d_j$, where the neuronal activity is given by $c = \sigma(m \cdot d)$, $\phi(c, \Theta_M) = c(c - \Theta_M)$, and Θ_M is a nonlinear function of some time averaged measure of cell activity, which in its simplest form is given by $\Theta_M = E[c^2]$, where E denotes the expectation over the visual environment. The transfer function σ is non symmetric around 0 to account for the fact that cortical neurons show a low spontaneous activity, and can thus fire at a much higher rate relative to the the spontaneous rate, but can go only slightly below it.

4 Results

4.1 Single Cell

In all the results reported here we used a fixed circular receptive field with diameter of 20 pixels. We tested the robustness of the results to receptive fields of sizes 10 to 30 pixels and got no qualitative difference in the results.

BCM neurons acquire selectivity to various orientations in the partial and the nonoverlapping case as well. When receptive fields are misaligned, various ocular dominance preferences may occur even for the same overlap. This result stands in sharp contrast to the one obtained by PCA neurons; only binocular neurons with a preferred horizontal direction emerge under for the PCA rule.
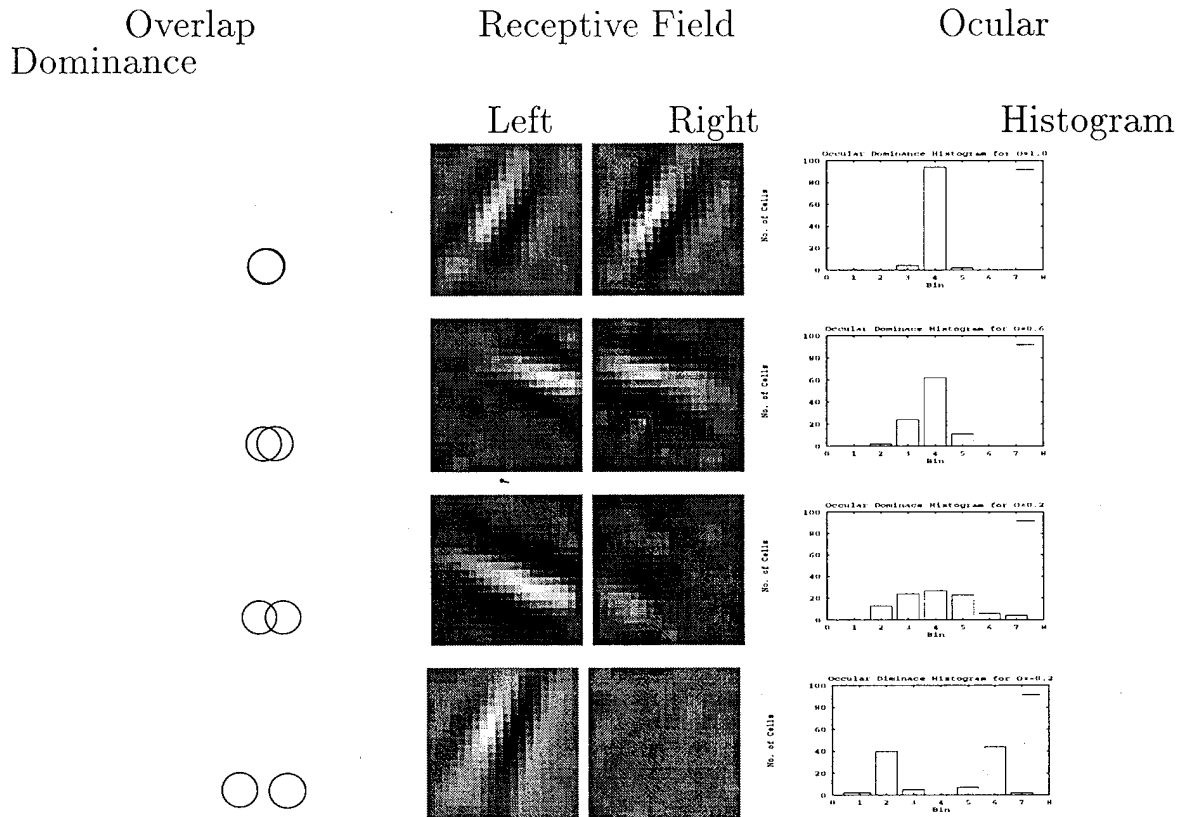
Figure 3: BCM neurons with different overlap values; $O = 1, 0.6, 0.2, -0.2$ from top to bottom. The ocular dominance histograms summerise the ocular dominance of 100 cells at each overlap value. The dependency of ocular dominance on visual overlap is evident.

The BCM receptive field formation results are summarized in Figure 3. Receptive field misalignment does not affect orientation selectivity of the dominant eye, but does produce varying degrees of ocular dominance; this depends on the degree of overlap between the receptive fields. The main result is that ocular dominance depends strongly (even for single cell simulations) on the degree of overlap between visual input to the two eyes.

The PCA results are presented in Figure 4. As mentioned above, it can be seen that the degree of overlap between receptive fields does not alter the optimal orientation, so that whenever a cell is selective its orientation is in the horizontal direction. The degree of overlap does affect the shape of the receptive fields, and the degree of orientation selectivity that emerges under PCA: orientation selectivity decreases as the amount of overlap decreases. However, when there is no overlap at all, one again gets heigher selectivity. For PCA, there is also a symmetry between the receptive fields of both eyes. This arises from invariance to a parity transformation defined in the appendix, that imposes binocularity.

We also studied the possibility that under the PCA rule, different orientation selective cells would emerge if the misalignment between the two eyes was in the vertical direction, but this produced horizontal binocular cells as well.
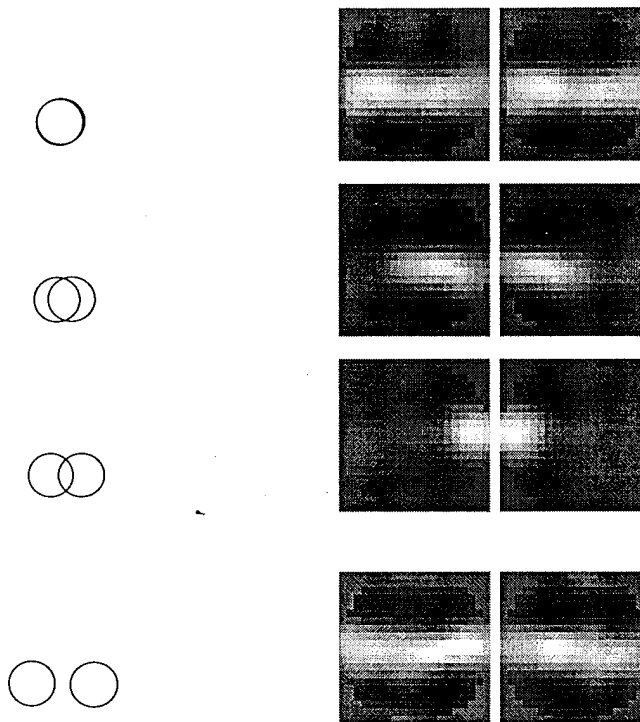
Figure 4: *Receptive fields for partially overlapping inputs using the PCA rule, Receptive field for an overlap value of $O = .6$ (top left). Receptive field for a small overlap, $O = .2$ (top right). Receptive field for no overlap , $O = -.2$ (bottom left). Receptive field for shift in the vertical direction between the visual inputs when $O = .5$ (bottom right). In all cases the cell is binocular and horizontal. The symmetry property evident in these receptive fields is analyzed in Shouval et. al. (1995).*

The PCA results described above were quite robust to introduction of nonlinearity in cell's activity; there was no qualitative difference in the results when a non symmetric sigmoidal transfer function was used.

4.2 Networks

In order to examine how network interactions effect these results we have run simulations of networks of interconnected neurons with both learning rules. We used a center surround interaction function I, and partially overlapping circular synaptic density functions A. We have taken the network response at point $\mathbf{r}$, $C(r)$ to be $C(\mathbf{r}) = \sigma\left(c(\mathbf{r}) + \sum_{\mathbf{r}'} I(\mathbf{r} - \mathbf{r}')c(\mathbf{r}')\right)$, where $c(\mathbf{r})$ is the single neuron response at point $\mathbf{r}$. In figure 4.2 we have compared the results for the two types of networks: PCA and BCM. We can see that these results are dominated by the single cell results. Networks of BCM neurons attain a higher degree of ocular dominance and a broader range of orientation preference.

5 Discussion

In this paper we contrast the consequences of a real visual environment on two learning rules, PCA and BCM, for a single cell. We show that the BCM neuron develops orientation selective cells to all orientations as well as varying ocular dominance. This is consistent with observation. In contrast the PCA neuron is unable to develop cells selective to all orientations and the cells are always binocular. All PCA neurons develop receptive fields that are symmetric under a parity transformation.

The Network results displayed here are dominated by single cell results; Networks of BCM neurons exhibit orientation and ocular dominance columns, whereas PCA networks are mostly binocular, and dominated by the horizontal orientation.

A recent paper by Erwin, Obermayer and Schulten (1995) , has compared the predictions of many models to experimental results. This comparison is different then ours in that it concentrates on organization of receptive fields across the cortex, rather then on the properties of the receptive fields themselves. In that paper very different types of models were compared, and the underlying assumptions of each model were different form each other. We in contrast compared and analyzed only two models, under the same set of realistic assumptions. However, Erwin et. al. also attempted to combine the two network models proposed by Miller, and they too report that in the parameter regime they have examined, they have failed to produce both ocular dominance and orientation maps. These results can also be understood in light of the single cell results for this type of input. The symmetry properties outlined in the appendix apply to this correlational model as well.

6 Acknowledgments

A Appendix: Symmetry properties of the eigenstates of the two eye problem

The evolution of neurons in a binocular environment under the PCA learning rule reaches a fixed point when $\mathbf{Q}\mathbf{m} = \lambda\mathbf{m}$. where $\mathbf{m}^T = (\mathbf{m}^l, \mathbf{m}^r)$, the left and right eye synaptic strengths, and $\mathbf{Q}$ is the two-eye correlation function. By Q_{ll} and Q_{rr} we denote the correlation functions withing the left and right eyes, and by Q_{lr} and Q_{rl} the correlation functions between left-right and right-left eyes.

We denote by upper case $R's$ the coordinates in each receptive field with respect to a common origin, and by lower case $r's$ the coordinates from the centers of each of the receptive fields. Thus R_{0l} and R_{0r} are the coordinates of the centers of the left and right eyes, R_l and R_r are the coordinates of points in both receptive fields, and $\mathbf{r}_l$ and $\mathbf{r}_r$ are the coordinates of the same points with respect to the centers of the left and right receptive field centers. For a misalignment s between receptive field centers, $R_{0l} + \mathbf{s} = R_{0r}$, therefore $R_r - R_l = R_{0r} - R_{0l} + \mathbf{r}_r - \mathbf{r}_l = \mathbf{s} + \mathbf{r}_r - \mathbf{r}_l$

Using translational invariance, it is easy to see that $Q_{ll} = E\left(d(\mathbf{r}_l)d(\mathbf{r}_l')\right) = Q(\mathbf{r} - \mathbf{r}')$ $Q_{rr} = E\left(d(\mathbf{r}_r)d(\mathbf{r}_r')\right) = E\left(d(\mathbf{r}_l + \mathbf{s})d(\mathbf{r}_l' + \mathbf{s})\right) = Q(\mathbf{r} - \mathbf{r}')$ $Q_{lr} = E\left(d(\mathbf{r}_l)d(\mathbf{r}_r')\right) = E\left(d(\mathbf{r}_l)d(\mathbf{r}_l' + \mathbf{s})\right) = Q(\mathbf{r} - \mathbf{r}' + \mathbf{s})$ $Q_{rl} = E\left(d(\mathbf{r}_r)d(\mathbf{r}_l')\right) = E\left(d(\mathbf{r}_l + \mathbf{s})d(\mathbf{r}_l')\right) = Q(\mathbf{r} - \mathbf{r}' - \mathbf{s})$ where E denotes an average with respect to the environment and where, occasionally, for simplicity, we replace $\mathbf{r}_l$ by $\mathbf{r}$. Since $Q(\mathbf{r} - \mathbf{r}') = E\left(d(\mathbf{r}_l)d(\mathbf{r}_l')\right)$ then $Q(\mathbf{r} - \mathbf{r}') = Q(\mathbf{r}' - \mathbf{r})$.

We now introduce a two-eye parity operator $\mathbf{P}$, which inverts the coordinates, as well as the two eyes:

$$\mathbf{P} : \begin{cases} \mathbf{r}_l \Rightarrow (-\mathbf{r}_l) \\ \mathbf{r}_r \Rightarrow (-\mathbf{r}_r) \\ \mathbf{s} \Rightarrow (-\mathbf{s}) \end{cases} \tag{A.1}$$

It follows that under $\mathbf{P}$ $\quad R_l - R_r = \mathbf{r}_r - \mathbf{r}_l + \mathbf{s} \Rightarrow -\mathbf{r}_r + \mathbf{r}_l - \mathbf{s}$

The two-eye parity operator can also be written in matrix form in terms of the one eye parity operator P, thus

$$\mathbf{P} = \begin{pmatrix} 0 & P \\ P & 0 \end{pmatrix}. \tag{A.2}$$

The effect $\mathbf{P}$ on the two-eye receptive fields $\mathbf{m}$ is

$$\mathbf{P} \begin{pmatrix} m^l(\mathbf{r}_l) \\ m^r(\mathbf{r}_r) \end{pmatrix} = \begin{pmatrix} m^r(-\mathbf{r}_l) \\ m^l(-\mathbf{r}_r) \end{pmatrix}$$

Any correlation function that is invariant to a two-eye parity transformation $\mathbf{P}$, has eigen-functions $\mathbf{m}^T(\mathbf{r}) = \big(m^l(\mathbf{r}_r), m^r(\mathbf{r}_l)\big)$, that are also eigen-functions of $\mathbf{P}$. This imposes symmetry constraints on the resulting receptive fields that force them to be binocular.

Any correlation function of the form

$$\mathbf{Q} = \begin{pmatrix} Q(\mathbf{r} - \mathbf{r}') & Q'(\mathbf{r} - \mathbf{r}' + \mathbf{s}) \\ Q'(\mathbf{r} - \mathbf{r}' - \mathbf{s}) & Q(\mathbf{r} - \mathbf{r}') \end{pmatrix} \tag{A.3}$$

is invariant to the two-eye parity transform $\mathbf{P}$ (that is $\mathbf{PQP} = \mathbf{Q}$), as long as $Q(\mathbf{x}) = Q(-\mathbf{x})$ and $Q'(\mathbf{x}) = Q'(-\mathbf{x})$.

Thus the eigen-functions of $\mathbf{Q}$, are also eigen-function of $\mathbf{P}$. The eigen-value is ± 1, Since $P^2 = 1$. Therefore we deduce that

$$\begin{pmatrix} \mathbf{m}^l(\mathbf{r}_l) \\ \mathbf{m}^r(\mathbf{r}_r) \end{pmatrix} = \pm \begin{pmatrix} \mathbf{m}^r(-\mathbf{r}_l) \\ \mathbf{m}^l(-\mathbf{r}_r) \end{pmatrix}. \tag{A.4}$$

Thus

$$\mathbf{m}(\mathbf{r}) = \begin{pmatrix} \mathbf{m}^l(\mathbf{r}_l) \\ \pm\mathbf{m}^l(-\mathbf{r}_r) \end{pmatrix}. \tag{A.5}$$

This means that the receptive fields for the two eyes are inverted versions of each other up to a sign. Therefore for this learning rule the receptive fields are always perfectly binocular.

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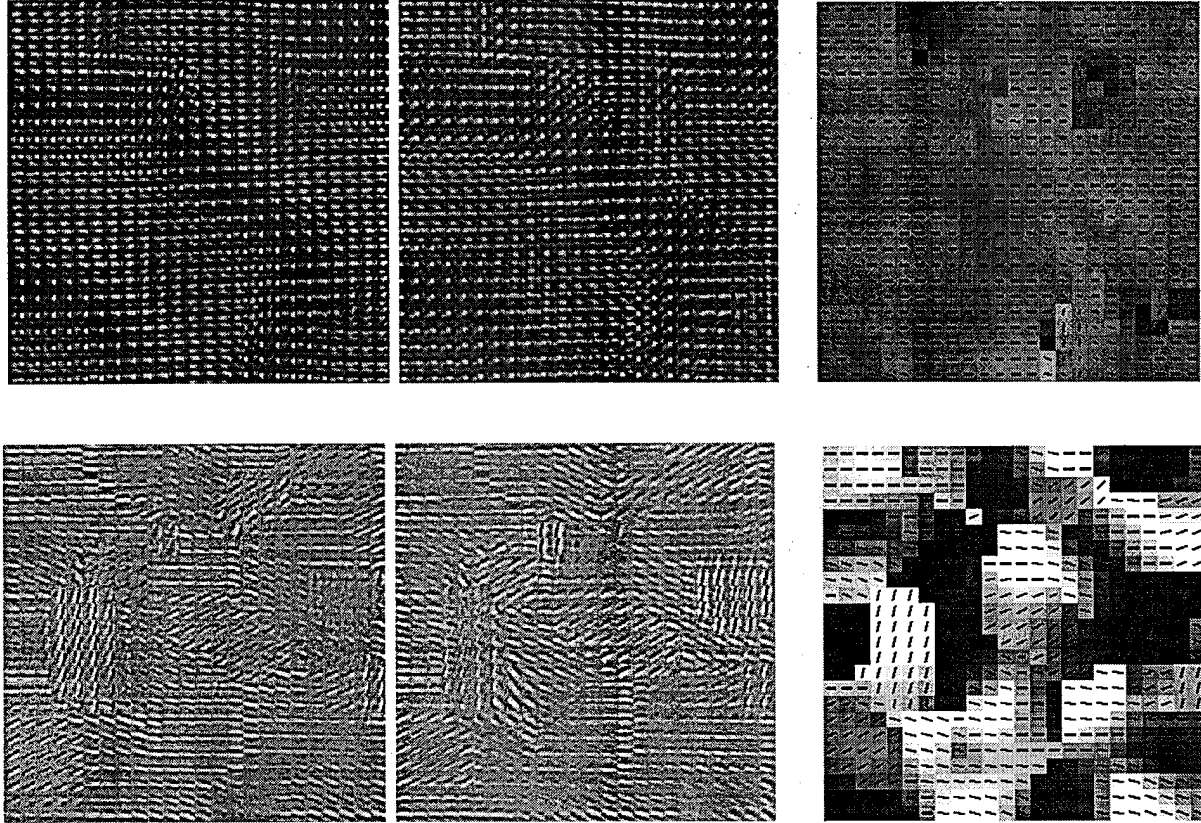
Figure 5: Comparison of Networks of PCA neurons (top) and BCM neurons (bottom). Network sizes are 24 X 24 Neurons, the interaction function is a balanced difference of Gaussians with $\sigma_1 = 1.5$ and $\sigma_2 = 3.5$. The center of each synaptic density function A is shifted by one pixel with respect to it's neighbour, the diameter of A is 18 pixels and the shift between the two eyes 16 pixels. On the left the feed forward Receptive fields for the left eye is presented, in the center for the right eye. On the right the joint results are presented, where the gray level of the backgrownd codes ocular preference, the orientation of the bar codes orientation preference, and it's length the degree of selectivity.